

Review Article

The invasive mysid *Hemimysis anomala*: an up-to-date review of its biology, ecology, distribution and ecological impacts

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Abstract

The “bloody-red shrimp” species *Hemimysis anomala*, native to the Ponto-Caspian Region, has spread rapidly and adapted over recent decades to new aquatic ecosystems worldwide, causing many ecological alterations. The reported impacts associated with this invasion are numerous, including overall food web structure modifications. This review focuses on *H. anomala*, examining its biology, ecology, distribution and ecological impacts. The species’ rapid success is attributed to its high fecundity, fast growth rates and broad adaptability to various habitats. Recent observations suggest that its distribution may expand further, especially in Western European lakes, reservoirs and the Laurentian Great Lakes. We present insights into its habitat, seasonal dynamics and influence on trophic interactions within native zooplankton communities. Additionally, we discuss methods used to study *H. anomala*, including citizen-science initiatives that enhance data collection and community engagement. The objective of this research is to provide up-to-date pieces of information on *H. anomala*’s ecology, including new data on its habitat preferences collected through scientific diving and participatory research. By characterising the spatial and temporal variation in its occurrence and abundance, we identify key environmental and biotic factors that may limit or support its further spread. We also highlight knowledge gaps and research priorities for future studies to better assess its impacts on the food webs of invaded ecosystems.

Key words: Bloody-red shrimp, exotic species, freshwaters, invasion dynamics, non-native



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Introduction

Freshwater ecosystems are amongst the most affected environments by invasive* species globally (IPBES 2023), resulting in significant ecological, economic and potentially public health impacts, as well as conservation challenges (Diagne et al. 2021; Gippet et al. 2023). Invasive species contribute to biodiversity loss, with freshwater ecosystems experiencing the greatest declines (Reid et al. 2019). These species can drastically alter ecosystem structure and function, especially under the pressures of climate change, which is increasing both the frequency of

* We acknowledge the current evolution of the definition of the term ‘invasive’ in the field of ecology. For the purpose of this paper, the term invasive is used to characterise a species that causes ecological or economic harm in a new environment where it is not native.

climate-related disturbances and temperatures favourable to invasions. Understanding invasion processes and predicting their impacts are essential for assessing risks and developing effective management strategies (Moyle and Marchetti 2006; Occhipinti-Ambrogi 2007; Vilizzi et al. 2021). The successful establishment of a potentially invasive species in a new environment is often linked to its life-history traits (also referred as species invasiveness) and other biological characteristics or again to ecosystem invasibility and ecological opportunity, which together facilitate its acclimatisation and integration into the invaded environment (Shea and Chesson 2002; Daly et al. 2023; Su et al. 2023).

The Ponto-Caspian Region, encompassing the Black Sea, Sea of Azov and Caspian Sea, is a significant source of invasive species, particularly crustaceans, which have proliferated within freshwater ecosystems in both Europe and North America (Soto et al. 2023). Amongst these species, the “bloody-red shrimp”, *Hemimysis anomala* (G. O. Sars, 1907), has shown rapid range expansion over recent decades, primarily colonising lentic ecosystems such as lakes, canals and river backwaters (Salemaa and Hietalahti 1993; Bij de Vaate et al. 2002; Lantry et al. 2010; Wittmann et al. 2016). Initially introduced to enhance food availability for fish production in ponds across regions of the former Soviet Union (Arbačiauskas et al. 2010), the species’ spread was significantly facilitated by the opening of the Main-Danube Canal in 1992. This event enabled the dispersal of *H. anomala* and other Ponto-Caspian species across Europe, mainly through the discharge of ballast water from shipping vessels (Leuven et al. 2009; Minchin and Boelens 2010). The successful invasion of *H. anomala* can be attributed to its high dispersal capability, fecundity, rapid growth rate and ability to colonise habitats with limited trophic resources, whether natural or anthropogenic (Dobrzycka-Kraheil et al. 2023; Oliveira et al. 2023). Furthermore, its broad tolerance to variations in temperature and salinity has bolstered its invasive success (Soto et al. 2023). The introduction of Mysidae into lake ecosystems has a well-documented history of unintended ecological consequences. For instance, from the 1950s to the 1980s, *Mysis diluviana* was deliberately introduced into North American lakes and reservoirs to enhance fisheries, yet these introductions frequently resulted in trophic disruptions rather than benefits (Fredrickson 2017). As an efficient zooplanktivore, *M. diluviana* out-competed juvenile planktivorous fish, altering trophic cascades that restructured entire food webs. In Flathead Lake (Montana), its introduction drastically reduced zooplankton biomass, leading to the collapse of native salmonid populations (*Oncorhynchus nerka*) and subsequent declines in higher predators (Ellis et al. 2011; Devlin et al. 2017). While *H. anomala* shares some ecological traits with *M. diluviana*, it thrives in warmer temperatures, favours littoral and nearshore environments and is an opportunistic omnivore rather than primarily zooplanktivorous (Kipp and Ricciardi 2007; Walsh et al. 2012). These situations underscore the profound and often unpredictable ecological impacts of invasive mysids, emphasising the need for a cautious assessment of *H. anomala*, whose long-term effects remain unexplored and consequently insufficiently understood. Recent observations indicate that the invasion of *H. anomala* is not a localised phenomenon, but a rapidly evolving issue with significant implications for aquatic ecosystems. In Europe, the species has been recorded in a variety of waterbodies, exhibiting an alarming trend in its spread. Notably, recent sightings have expanded to new areas, including lakes in France and Germany and large freshwater reservoirs in the United Kingdom (Frossard and Fontvieille 2018; Andrews et al. 2023; Dickey et al. 2024). In North

America, *H. anomala* was first reported in the Laurentian Great Lakes in 2006 and has since been detected in all five Great Lakes, with the latest discovery in Lake Superior (Marty et al. 2010; Evans et al. 2018). Its recent presence in Lake Michigan harbours further confirms its establishment nearly a decade post-discovery. The rapid establishment of *H. anomala* across various hydrological systems and habitats underscores the urgent need for global monitoring and management strategies to mitigate its impact on local ecosystems.

This study provides a comprehensive review of the current knowledge on the ecology of *H. anomala*. Our investigation includes novel data on the species' habitat preferences, collected through a participatory research approach involving both scientific and French recreational divers. This collaboration facilitated data collection across diverse aquatic environments and promoted community engagement in ecological research, enhancing the monitoring of *H. anomala* populations. Additionally, we assess various methodologies for studying this invasive species, including field observations and sampling techniques. This comparative analysis identifies the most effective methods for detecting *H. anomala* and documenting its spread. By characterising spatial and temporal variations in its occurrence and abundance, we highlight key environmental and biotic factors influencing its further spread. Finally, we identify knowledge gaps and research priorities essential for future investigations into the impacts of *H. anomala* on the food webs of invaded ecosystems.

Material and methods

To support our study of *H. anomala*, a comprehensive literature review was conducted to establish a baseline on the ecological characteristics of the species and gather relevant pieces of information from newly-invaded sites. Initially, the literature review was performed using the Web of Science (WoS, Clarivate Analytics, Philadelphia, USA) databases up to spring 2024, with an update in autumn 2024. A search in Scopus did not yield any additional articles. The literature search employed the following keyword strings: “*Hemimysis*” and “*anomala*” or “Blood* Red” and “Shrimp” or “Blood* red” and “Mysid*” for the title, abstract and keywords. These keywords were selected to capture a broad range of publications, from studies focused specifically on the species to more general discussions. The results from this search underwent exhaustive analysis, encompassing articles published from May 1993 to October 2024 (Suppl. material 1: fig. S1). Additionally, a thorough review of the references and citations of the initially selected papers identified 31 additional articles that provided relevant insights not directly accessible through database searches.

Results and discussion

Mysids belong to the order Mysida, comprising approximately two families, 179 genera and 1,210 species, distributed across a wide range of aquatic ecosystems and habitats (Oliveira et al. 2023). Within this diverse group, the majority of species inhabit marine environments, with only about twenty species found in freshwater and brackish habitats (Mauchline 1980). According to Lunina et al. (2019), the genus *Hemimysis* (family Mysidae) includes 11 species found in marine, brackish and freshwater environments, predominantly inhabiting caves, bottom and demersal regions. Amongst these species is *Hemimysis anomala* (Suppl. material 1: fig. S2), first described by Sars (1907).

Spatial distribution

Native range

Hemimysis anomala originates from the estuaries of the Black Sea, Sea of Azov and Caspian Sea (Fig. 1). It is present at the base of rivers flowing into these seas and in brackish waters. Since the 2000s, *H. anomala* has been reported worldwide, following intentional or accidental introductions (Audzijonyte et al. 2008). Paradoxically, *H. anomala* is recognised as critically endangered in its native habitat (Alexandrov 1999; FAO 2005). This situation illustrates how specific environmental pressures and habitat changes can threaten a species in one context while being considered invasive in another, thereby creating a conservation paradox (Marchetti and Engstrom 2016). In its native range, *H. anomala* faces severe threats from habitat loss, pollution and ecological disturbances (Korzhov 2021). These disturbances, amplified by industrial and agricultural activities (e.g. hydrocarbons, agricultural runoff), alter essential conditions for its survival, impacting water quality and diminishing natural resources and habitats needed by native crustaceans (Zaitsev et al. 2002; Gogaladze et al. 2021; Korzhov 2021). Furthermore, invasive species and ecological shifts heighten competition for resources, further compromising the viability of native populations (Son et al. 2020; Gogaladze et al. 2021).

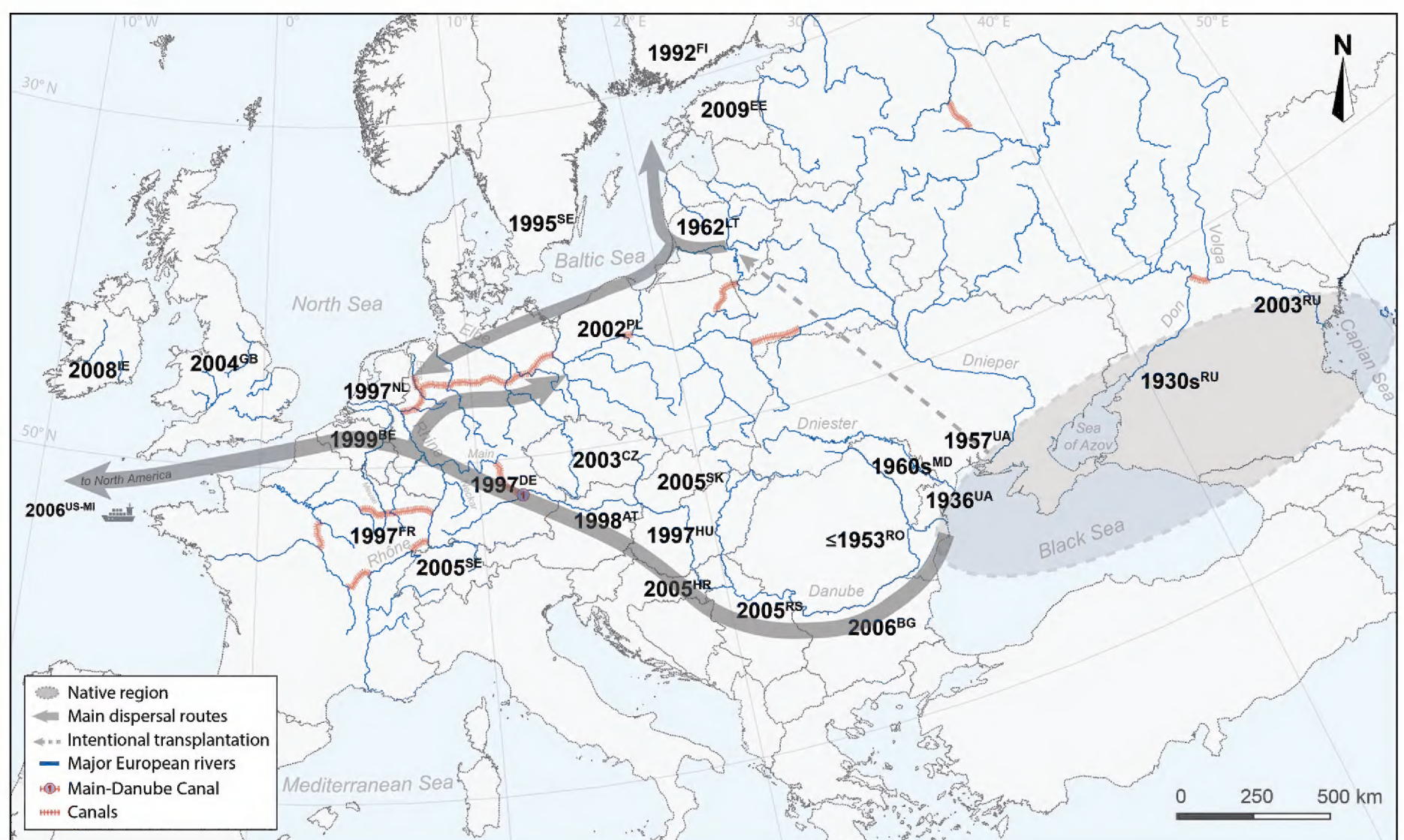


Figure 1. Map showing the distribution and dispersal periods of *Hemimysis anomala* in Central and Western Europe from the Ponto-Caspian area (Black, Azov and Caspian Seas). The shaded area refers to the presumed native range of *H. anomala* (Ponto-Caspian). Wide grey arrows depict the main dispersal routes and dashed grey arrows indicate intentional translocation to the Kaunas water reservoir in Lithuania (adapted from Audzijonyte et al. (2008)). Solid blue lines represent major European rivers capable of supporting the dispersal of *H. anomala*, while dashed red lines represent canals that have facilitated its spread. The ship pictogram indicates transatlantic transport via ballast water discharge to North America, with the first records of *H. anomala* in Lake Michigan in 2006, likely resulting from multiple European introduction sources (Audzijonyte et al. 2008). Years indicate first records followed by letters indicate the ISO codes of the corresponding country (see Suppl. material 1: table S1).

This duality highlights the complex management requirements for *H. anomala*, where its conservation is critical in its native habitat, but it poses a significant ecological challenge as an invasive species elsewhere.

Spread in Europe

In Europe, the expansion of *H. anomala* and its rate of spread through freshwater ecosystems have been facilitated by human activities since the 1940s (Wittmann 2007). The species was intentionally introduced into large lakes and reservoirs within the former Soviet Union, beginning with the Dniepr Reservoir in Ukraine in the late 1950s and followed by the Kaunas Reservoir in Lithuania in 1960, to serve as fish food (Horecký et al. 2005; Arbačiauskas et al. 2010). These introductions were part of a broader acclimatisation effort conducted between 1955 and 1989 to increase the biomass of commercially important fish species (Karpevich 1975). From the Kaunas Reservoir, *H. anomala* began its expansion into the Baltic Basin via natural dispersal and anthropogenic corridors, including the Curonian Lagoon and connected waterways (Audzijonyte et al. 2008; Arbačiauskas et al. 2017). Molecular analyses confirmed that the Lithuanian populations played a key role as a secondary source for the species’ expansion into the Baltic Sea (Audzijonyte et al. 2008). Its ability to tolerate brackish environments (Table 1) facilitated its establishment in the Baltic Sea, where the first observation was recorded in 1992 in the coastal waters of south-western Finland (Salemaa and Hietalahti 1993). Subsequent sightings occurred along the Swedish coastline in 1995, in the Gulf of Gdańsk in Poland in 2002 (Janas and Wysocki 2005) and in Estonian waters in 2009 (Kotta and Kotta 2010). The rapid rate of expansion, confirmed retrospectively in Hungary in 1997, observed in 1998 in Austria and later in 2005 in Slovakia, can be attributed to the release of ballast water from shipping vessels (Wittmann et al. 1999; Wittmann 2007; Borza 2008; Borza et al. 2011). During the early 1990s, the intensification of river traffic across Eastern and Central Europe facilitated the spread of *H. anomala* via the Danube-Black Sea Canal, which connects the Danube River to the Black Sea and its tributaries (Kotta and Kotta 2010). The spread was further enabled by the construction of numerous canals, notably the Main-Danube Canal, which was completed in 1992 and links the Danube to the Rhine Rivers and allows the passage of large vessels from the Black

Table 1. Hydrological and physico-chemical amplitudes of *Hemimysis anomala* (Băcescu 1940; Ketelaars et al. 1999; Wittmann 2007; Ellis and MacIsaac 2009; Wittmann and Ariani 2009), including mean and standard deviation ($m \pm S.D$) for specific parameters (data from Wittmann 2007).

Parameter	$m \pm S.D$	Value (min.-max.)
Depth (m)	4.04 ± 5.42	< 1–60
Temperature (°C)	17.21 ± 4.47	2–28
Dissolved oxygen (mgO ₂ /l)	7.197 ± 1.42	3.99–13.92
Carbonate hardness (°d)	8.642 ± 0.98	6–12
Conductivity (µS/cm)	3792 ± 6947	98–29200
Water pH (pH)	7.87 ± 0.50	6.21–8.65
Salinity (‰)	2.14 ± 4.21	0–18
Water Current (m/s)	0.15 ± 0.22	0–0.81
Turbidity (NTU †)	28.61 ± 26.29	5–137

Note: † Nephelometric Turbidity Units.

Sea to the North Sea (Fig. 1). The pathway, often referred to as the “southern corridor”, further facilitated the spread of the species (Audzijonyte et al. 2008). Beyond continental Europe, the first reports were from the English Midlands in the United Kingdom in 2004 (Holdich et al. 2006), followed by sightings in southeast England in 2020 (Andrews et al. 2023). In Ireland, the first reports date back to 2008, in the basin of the River Shannon, from which the species spread to Northern Ireland (Minchin and Holmes 2008; Minchin and Boelens 2010; Gallagher et al. 2015). Unlike in North America, *H. anomala* has mainly colonised watercourses rather than lake ecosystems in Europe (Verslycke et al. 2000; Janas and Wysocki 2005). The first observation of the crustacean in the Rhine Basin (in Germany and the Netherlands) was made in the Neckar River in 1997 and in the Main River in 1998 (Schleuter and Schleuter 1998; Schleuter et al. 1998; Kelleher et al. 1999). It then continued to spread rapidly in the waterways of north-eastern and southern Germany, as well as in the River Meuse in southern Belgium, with sightings in the Galgenweel, near the Westerschelde Estuary and in the Netherlands (Eggers et al. 1999; Verslycke et al. 2000; Vanden Bossche 2002; Rudolph and Zettler 2003; Stich et al. 2009). The southern corridor has been *H. anomala*’s most likely route into France, where the first observations were made in the Rhône in 2003 (Daufresne et al. 2007) and in the Rhine in 2005 (Dumont 2006). *Hemimysis anomala* may have now established throughout the Paris region and northern France, extending as far as the Rhône Delta in the Mediterranean (Wittmann and Ariani 2009; Dumont and Muller 2010). In the large and deep peri-alpine lakes of France, while the species has colonised Lake Bourget and Lake Geneva since 2007 (Golaz and Vainola 2013; Frossard and Fontvieille 2018; Lods-Crozet 2020), the first individuals were only recently discovered in Lake Annecy in early 2024, likely due to this system being disconnected from the Rhône River (SILA, pers. com. 2024). The identification of *H. anomala* in Lake Stechlin in Germany in 2023 now raises concerns about its spread and potential impact on local biodiversity (Dickey et al. 2024).

Spread in North America

Hemimysis anomala was first observed in Lake Ontario in the Great Lakes region of North America in 2006 (Ricciardi 2006; Kipp and Ricciardi 2007; Marty et al. 2010), prompting the establishment of a monitoring network to document and assess its expansion across the continent (Suppl. material 1: fig. S3). The species has since colonised other large lakes (Michigan, Muskegon) via their connecting rivers (Pothoven et al. 2007), as well as the St. Lawrence River near Montreal, Canada (Kestrup and Ricciardi 2008; de Lafontaine et al. 2012). Similar to Europe, the arrival and further invasion of *H. anomala* were facilitated by ballast water exchanges from multiple European source regions. Genetic analyses confirmed that North American populations originated from both Danubian and Baltic lineages (Audzijonyte et al. 2008; Questel et al. 2012), suggesting repeated introductions through ballast water releases. By 2018, it had been found in all five Laurentian Great Lakes (Suppl. material 1: fig. S3; Evans et al. (2018)).

Introduction vectors in isolated environments

Although the spread of *H. anomala* has been mainly facilitated by ballast water, other introduction vectors must be considered in isolated environments like Lake Annecy. Amongst these vectors, recreational activities such as boating, diving and

fishing can play a significant role (Martínez-Laiz et al. 2019; Morreale et al. 2023). The passive transport of aquatic organisms via contaminated watercraft and biofouling on boat hulls, especially in the absence of strict cleaning protocols, provides an effective mode of dispersal (Kelly et al. 2013; Mohit et al. 2023). Furthermore, fish stocking and the transport of live fish represent an important anthropogenic vector, as the water used in transport can harbour larvae or juveniles of *H. anomala* (Zajicek et al. 2009; Saccà 2015; Olden et al. 2021). Strengthening regulations on fish transport and ensuring water treatment or filtration before discharge could help mitigate this risk. Lastly, although natural vectors are less studied, extreme weather events such as flooding and passive dispersal by aquatic birds (especially migratory species) could serve as secondary mechanisms of transport, leading to the accidental introduction of these organisms into new habitats (Andrews et al. 2023). These factors highlight the need for comprehensive management strategies to mitigate the risks of *H. anomala* introductions.

Comparative analysis of sampling methods and advanced analytical approaches

Most studies conducted between the early 1990s and 2010 focused on describing the expansion and ecology of *Hemimysis anomala* (Salemaa and Hietalahti 1993; Verslycke et al. 2000). In the large North American lakes, study sites were selected, based on the preferred habitats of *H. anomala*, with individuals often collected by deploying a plankton net from the surface (Marty et al. 2010; Taraborelli et al. 2012). In other colonised habitats such as rivers, canals and artificial shelters, various methods have been used or developed to detect, sample and quantify their abundance, including direct observations at night using torchlight (Holdich et al. 2006; Stubbington et al. 2008), light-based traps (Brown et al. 2017), baited traps (Odenwald et al. 2005), hand nets (Faasse 1998; Janas and Wysocki 2005; Pothoven et al. 2007), dredging (Kotta and Kotta 2010), direct observation and sampling using a home-made collector by diving (Dumont 2006; Dumont and Muller 2010; Jacquet 2023; Frossard et al. 2023), environmental DNA (eDNA) (Oyagi et al. 2017) and, more recently, high-resolution acoustic cameras (multibeam sonar; Rogissart et al. (2024)).

The use of light, such as torchlight, can be highly effective in detecting the presence or absence of *H. anomala* in shallow waters, although turbidity can restrict this approach (Stubbington et al. 2008). Sampling using baited bottles containing algae tablets (*Spirulina* 20%) intended for aquarium fish has also proved effective overnight at shallow depths (Odenwald et al. 2005). However, using pieces of fresh pig's liver can lead to significant oxygen consumption in baited bottles, resulting in increased mortality (Odenwald et al. 2005). Although diving-based methods necessitate specific skills and, depending on the country, recognised certification, they enable direct observation, sampling and *in situ* experiments, although they remain rarely used in long-term studies (Dumont and Muller 2010; Frossard and Fontvieille 2018; Jacquet 2023). Diving can improve understanding of certain aspects of the animal's life, such as the proportion of females (e.g. with visible marsupial pouches) or juveniles or the seasonality of the appearance of swarms in monitored areas.

Although vertical nets and traps have been effective at night for assessing Mysidae populations (Brooking et al. 2010; Brown et al. 2017), more advanced methods have also emerged in recent years. Efforts have been made to use metabarcoding to detect *H. anomala* in Great Lake ecosystems or in Lake Geneva by analysing

the stomach contents of predatory fish, although its presence was not detected (Mychek-Londer et al. 2020; Rogissart et al. 2022).

Environmental DNA (eDNA) sampling, particularly when combined with quantitative PCR (qPCR) or droplet digital PCR (ddPCR), provides a highly sensitive, non-invasive method for detecting *H. anomala* in challenging environments such as ballast water and complex habitats, often missed by traditional methods (Oyagi et al. 2017; Cangelosi et al. 2024; Melliti et al. 2025). While eDNA-qPCR has great potential for early detection, environmental factors such as water flow, temperature and turbidity can affect detection rates and lead to false positives or negatives, as eDNA cannot distinguish between living and dead organisms (Oyagi et al. 2017; Cangelosi et al. 2024). Recent advances in ddPCR technology provide increased sensitivity for detecting low concentrations of eDNA and remove the need for calibration curves (Melliti et al. 2025). Therefore, eDNA serves as a valuable complementary tool to traditional methods in monitoring programmes. Additionally, Rogissart et al. (2024) demonstrated that using an acoustic camera can be a valuable non-invasive approach for monitoring and recording real-time behaviour of *H. anomala* in lake littoral zones.

Overall, integrating traditional and advanced sampling techniques enhances our understanding of *H. anomala*'s ecological impact on invaded ecosystems and underscores the importance of continued innovation in methods to more effectively monitor invasive species.

Habitat

Habitats with rocky substrates, such as those found in large lakes or ponds and built environments like concrete walls with cracks, provide favourable conditions for the establishment of this species (Kestrup and Ricciardi 2008; Marty et al. 2010; Walsh et al. 2010; Boscarino et al. 2020). Additionally, the arrangement of rocks, their diameter and the distance between them or between them and the benthic sediments influence the speed of colonisation by providing suitable habitats and substrates to facilitate their establishment and growth (Claramunt et al. 2012). Swarm areas are also larger in inland lakes than in coastal rivers (Kestrup and Ricciardi 2008). Observations of habitat preferences depend on the sampling methods: while the average swarm depth is around 30 m in North American studies, it exceeds 60 m in the initial studies conducted in the Ponto-Caspian Region and around the Black Sea (Zhuravel 1959). However, in general, *H. anomala* are thought to prefer sublittoral waters (< 40 m) (Ricciardi et al. 2012). Numerous swarms have been observed at depths < 12 m within and around beds of submerged branches or macrophyte *Myriophyllum spicatum* (Serge Dumont, pers. com.) and anthropogenic structures such as under pontoons, riprap, jetties, slipways and in tree roots along the banks (Stubbington et al. 2008). *Hemimysis anomala* primarily lives hidden, near or under benthic or artificial shelter and rocky substrates during the day, where it finds refuge from strong currents or predators (Ketelaars et al. 1999; Rogissart et al. 2024).

Diet and feeding behaviour

The diet of *H. anomala* was initially identified through analyses of stomach content analyses, stable isotopes and laboratory-based feeding experiments. Stable isotope analyses of stomach contents and microscopic examination of both *H. anomala* and its predators, along with DNA marker analyses specific for hard-to-analyse prey species

in gut contents, provide valuable insights into the trophic position of *H. anomala* (Evans et al. 2018; Frossard et al. 2023). Immunochemical gut content analysis using specific antisera complements these methods by enabling precise identification of prey species, thereby providing a more detailed and comprehensive understanding of the feeding ecology of *H. anomala* (Wachala et al. 2025). When coupled with regular seasonal sampling, these methods offer a clear picture of the trophic ecology and their role in native food web interactions (Lantry et al. 2012; Marty et al. 2012; Yuille et al. 2012; Evans et al. 2018; Frossard et al. 2023; Patonai et al. 2024).

Juveniles generally consume small zooplankton such as rotifers (Halpin et al. 2013) and phytoplankton (Ketelaars et al. 1999; Borcharding et al. 2006; Frossard and Fontvieille 2018). Phytoplankton can also be an important resource for all life stages, as observed in Lake Ontario (Evans et al. 2018). Adults primarily consume zooplankton, but, being cannibalistic, are also capable of consuming various organic remains (dead fish) (Ketelaars et al. 1999; Dumont 2006) and ingesting green algae (Lowery et al. 2023). Their maximum capacity to ingest algae is approximately 1,000 cells per animal per hour and 9,000 cells per ml at half-saturation (Lowery et al. 2023). Field observations suggest that *H. anomala* prefers cladocerans, regardless of their life stage (Halpin et al. 2013; Evans et al. 2018). These findings are supported by laboratory experiments in which *H. anomala* preferentially entered mesocosms with a majority of cladocerans as resources (Iacarella et al. 2015). *Hemimysis anomala* can consume prey up to 30% of its size, including *Bythotrephes longimanus* that is a crustacean predator (Evans et al. 2018). Its primary filter (structure enabling the filtration of food particles), with a mesh size of less than 1 µm, comparable to that of *Daphnia* spp., enables it to exploit a wide range of suspended particle sizes, potentially granting access to an abundant food source (Borza et al. 2024). Additional immunochemical analyses confirm its broad dietary range, which includes a wide variety of prey, including *Bosmina longirostris*, *Daphnia pulex*, veliger larvae of Dreissena mussels and copepods (Wachala et al. 2025).

Hemimysis anomala shows marked seasonal variations in its diet, closely linked to fluctuations in prey abundance, ranging from autotrophic protists to zooplankton (Evans et al. 2018; Frossard et al. 2023). This dietary flexibility enables *H. anomala* to adjust its feeding strategy according to seasonal and environmental variations, maximising its success in various invaded ecosystems (Patonai et al. 2024). The species is likely to utilise greater food abundance in spring and summer than in autumn and winter, showing a predominant dependence on the pelagic environment during summer and autumn (Frossard et al. 2023). Additionally, higher temperatures from spring to autumn tend to increase feeding rates in parallel with increasing metabolic demand, enhancing growth potential (Sun et al. 2013; Penk et al. 2016). *Hemimysis anomala* is often found close to the substrate, with a significant proportion of detritus in its stomach content, suggesting direct feeding on benthic substrates (Borcharding et al. 2006). However, the relative contribution of benthic and pelagic resources appears to vary depending on environmental characteristics and opportunities at study sites, demonstrating its significant dietary flexibility (Ives et al. 2013; Frossard and Fontvieille 2018; Patonai et al. 2024).

Spatio-temporal distribution and behaviour dynamics

The distribution and behaviour of *H. anomala* swarms exhibit significant spatio-temporal dynamics. The depth of plankton net catches according to the time of day or night during fishing revealed vertical variations in swarms during the day, even in a

marina with a maximum depth of around 2 m (Nunn and Cowx 2012). Catches appear to be much deeper and closer to the substrate during the day than at night. This circadian rhythm variation can be explained by the influence of light intensity and spectrum on the distribution and behaviour of swarms (Boscarino et al. 2012). Experiments exposing adults and juveniles to different light spectra of increasing intensity revealed that juveniles preferred brighter light sources than adults (10^{-3} and 10^{-7} mylux, respectively; ‘mylux’ measures brightness as perceived by the visual pigments of *H. anomala*, Gal et al. (1999)), with adults preferring to remain hidden during the day ($> 10^{-4}$ mylux for avoidance; Boscarino et al. (2020); Rogissart et al. (2024)).

Seasonal variations in swarm abundance and density have also been observed. Observations in Germany over one year (2005) revealed variations in abundance across different periods (Janas and Wysocki 2005). In summer, the proportion of adults was lower than juveniles and vice versa in winter. This dynamic is also observed in North America, where summer populations of *H. anomala* are predominantly composed of juveniles (< 6 mm), small adult males (~ 7 mm) and few reproductive females (5–10%). In winter, *H. anomala* forms swarms that can be observed in both Europe and North America, with densities peaking when temperatures are between 6 °C and 12 °C (Verslycke et al. 2000; Claramunt et al. 2012; Jacquet 2023; Rogissart et al. 2024). The size composition or sex/developmental stage of individuals present in these swarms do not differ from those of individuals sampled on the bottom, indicating that these aggregations are not specifically related to reproduction function (Wachala et al. 2025). This pattern can be explained by temperature influences, food availability and predator presence, as confirmed by both laboratory and field studies (Boscarino et al. 2020; Wachala et al. 2025). *Hemimysis anomala* can adapt to a relatively wide range of abiotic factors and environmental conditions, including low winter temperatures (Table 1; Pienimäki and Leppäkoski (2004)). Individuals exhibited sustained growth even during winter at the lowest temperatures ($0.011\text{--}0.015$ mm d $^{-1}$) and, contrary to previous assumptions, post-reproductive males do not die immediately after reproducing (Wachala et al. 2025). This ability to survive in cold waters aligns with observations from frozen (surface) lakes in France, where temperatures reach approximately 3 °C (Dumont 2006), suggesting high thermal tolerance and adaptation to prolonged winter conditions.

Once introduced into a habitat, *H. anomala* can spread in lentic environments, but is displaced by flowing water (Table 1), limiting its introduction into new ecosystems (Wittmann and Ariani 2009). However, the species has spread across England and the Baltic Region, demonstrating some ability to migrate upstream through unsuitable areas for permanent inhabitation (Stubbington et al. 2008). *Hemimysis anomala* may have a higher capacity to spread compared to other invasive Ponto-Caspian crustaceans, such as certain gammarids established in Europe and North America (Pienimäki and Leppäkoski 2004; Wittmann 2007).

Ecological impacts

Potential negative impacts

The ecological impacts of *Hemimysis anomala* establishment in receiving aquatic ecosystems are predominantly based on its high zooplankton consumption capacity (Borcherding et al. 2006; Ricciardi et al. 2012; Lowery et al. 2023). For instance, in the St. Lawrence River, densities of cladocerans, ostracods, rotifers and

predatory invertebrates decreased drastically in late summer, corresponding with the proliferation of Mysidae (Sinclair et al. 2016). Similarly, the abundance of cladocerans declined sharply following the invasion of Lake Honderd in the Netherlands by *H. anomala* (Ketelaars et al. 1999). This predation pressure can disrupt zooplankton community structure, potentially altering food web dynamics and impacting species dependent on zooplankton as a primary food source (Fig. 2).

In addition to predation, *H. anomala* may compete directly with native Mysidae for zooplankton, a competition intensified by *H. anomala*'s higher feeding rates relative to body mass compared to other Mysidae (Dick et al. 2013; Patonai et al. 2024). This competitive advantage is highlighted by the stronger functional response of *H. anomala*, where its higher attack rates and shorter handling times enable efficient predation, even in the presence of predators, distinguishing it from native Mysidae (Barrios-O'Neill et al. 2014; Penk et al. 2018). The species may also compete with other native macroinvertebrates with which it shares a trophic niche. However, *H. anomala*'s impact on such macroinvertebrates (e.g. gammarids) does not appear significant (Marty et al. 2010; Taraborelli et al. 2012). Further, in the gravel pits of Alsace (France), no significant impact of *H. anomala* on zooplankton resources or Hydra populations has been demonstrated, despite both species feeding on zooplankton and are present at the same depths (Dumont and Muller 2010).

Beyond trophic interactions, *H. anomala* exhibits the ability to ingest 30 µm plastic particles at a similar rate to microalgae, with a maximum ingestion of about 750 particles per animal per hour (half-saturated at 5,000 particles per ml) (Lowery et al. 2023). Furthermore, *H. anomala* was associated with high contaminant concentrations, including methylmercury (MeHg), exceeding that of other littoral invertebrates such as amphipods, dreissenid mussels and zooplankton (Zhang et al. 2012; Brown et al. 2022). This capacity raises concerns about the bioaccumulation of contaminants up the food chain, potentially impacting fish and other higher trophic levels. Due to its position in invaded food webs and its prevalence in some places, such as harbours, for instance, where high levels of organic and inorganic pollutants can be detected, *H. anomala* may contribute to the bioaccumulation of these pollutants. Furthermore, its presence can potentially elongate the food web by introducing additional trophic levels, thereby increasing the risk and magnitude of contaminant transfer to higher trophic levels. Additionally, its high lipid content not only facilitates the retention of organic contaminants, but also provides an energy-rich resource for consumers, raising questions about whether the overall impacts of *H. anomala* invasion on food webs are beneficial or detrimental.

Potential positive impacts

Despite the potential for negative impacts, *H. anomala* may contribute positively to certain ecosystems, especially as a food source for various fish species. Isotopic approaches and visual examination of stomach contents suggest that *H. anomala* can contribute to the diet of various fish species such as yellow perch (*Perca flavescens*), European perch (*Perca fluviatilis*), rock bass (*Ambloplites rupestris*), lake cisco (*Coregonus artedii*), white perch (*Morone americana*), alewife (*Alosa pseudoharengus*), largemouth bass (*Micropterus salmoides*) and rainbow smelt (*Osmerus mordax*) (Lantry et al. 2010; Yuille et al. 2012; Gallagher et al. 2015; Geisthardt et al. 2022). The contribution of *H. anomala* to fish diets appears positively correlated with its abundance and varied

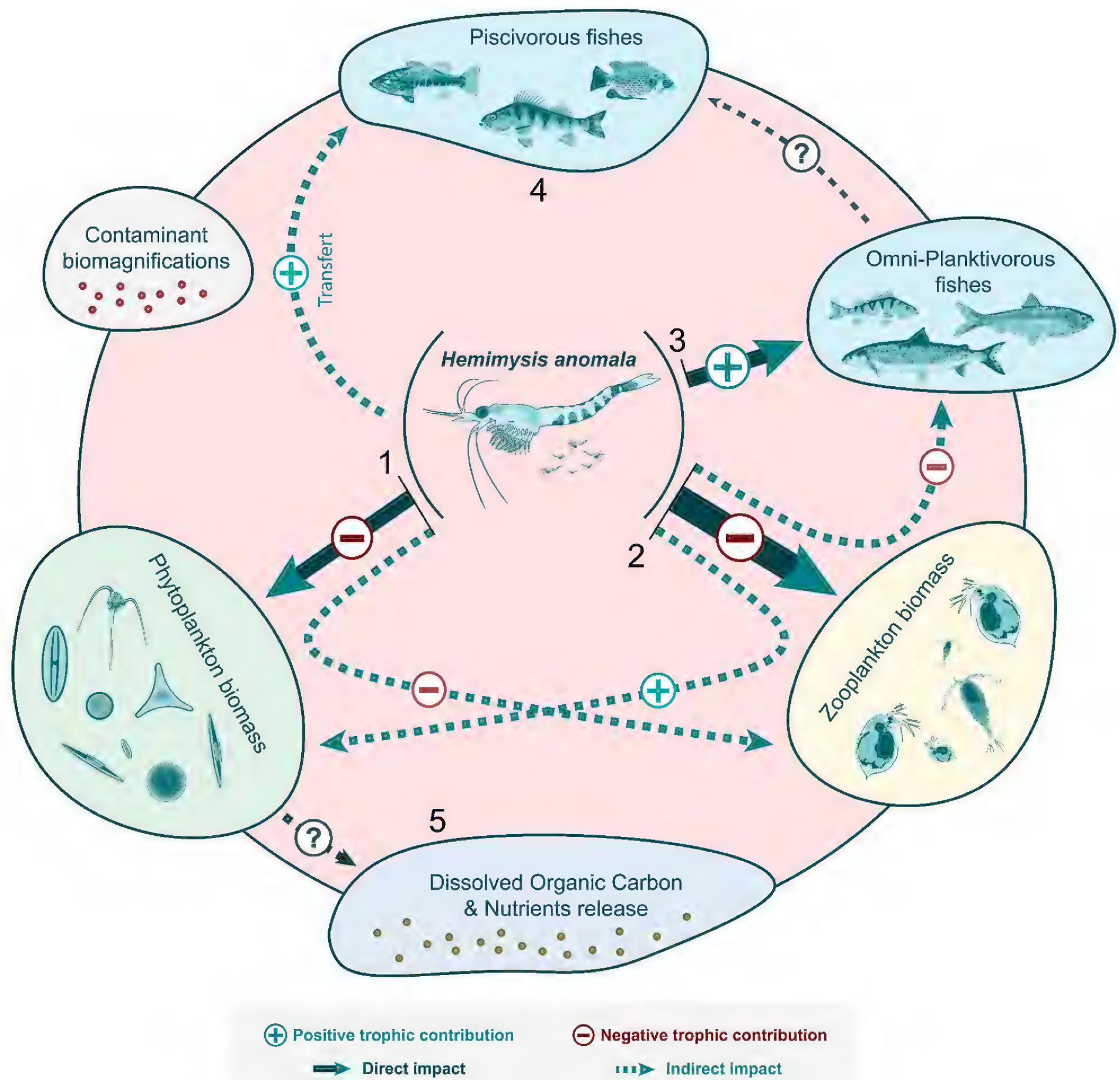


Figure 2. Impacts of *H. anomala* in aquatic food webs. *Hemimysis anomala* influences food web dynamics through multiple direct and indirect pathways leading interferences with different trophic levels. Solid arrows represent direct trophic interactions, while dashed arrows shown indirect effects. (1) *Hemimysis anomala* exerts a direct negative impact on phytoplankton through consumption, reducing its biomass that can trigger indirect negative impacts on zooplankton by lowering the availability resources; (2) *Hemimysis anomala* exerting a direct negative impact on zooplankton biomass by predation that can lead to a positive indirect effect on phytoplankton biomass by reducing grazing pressure from zooplankton. However, the decline in zooplankton may have negative indirect consequences for omni-planktivorous fishes, which rely on zooplankton as a primary food source; (3) *Hemimysis anomala* serves as a prey for omni-planktivorous fishes, potentially increasing their biomass (direct positive effect). However, by reducing zooplankton availability, *H. anomala* may impose an indirect negative effect on these fishes due to resource competition. As a consequence, the net effects of *H. anomala* on omni-planktivorous fishes remain to be clarified; (4) Due to the uncertainty of the lack of effect of *H. anomala* on omni-planktivorous fishes, the indirect effects of *H. anomala* on piscivorous fishes remain unclear. However, *H. anomala* may contribute to contaminant biomagnification by lengthening the food web ultimately impacting the extent of contamination of higher trophic levels; (5) *Hemimysis anomala* releases nutrients and dissolved organic carbon (DOC) through excretion and partial fragmentation of organic matter during feeding, which may stimulate primary production. This process may play a role in nutrient cycling and biogeochemical processes in aquatic ecosystems, though further research is also needed here to quantify its extent.

amongst seasons and years. However, it is important to note that, despite the presence of swarms of *Hemimysis* at the same sites, they are found in low quantities or even absent in the stomach contents of the round goby (*Neogobius melanostomus*) (Lantry et al. 2010; Fitzsimons et al. 2012; Geisthardt et al. 2022). Moreover, the high lipid concentration of these shrimps enables young perch to reach sexual maturity much more quickly than with a diet based on other prey (Zhuravel 1959; Borchertding et al. 2007). These observations suggest that *H. anomala* could have a significant impact on food web dynamics and the feeding ecology of fish in environments favourable to the species where it occurs at high abundance (Fig. 2; Geisthardt et al. (2022)).

Finally, *H. anomala*'s omnivorous feeding habits, combined with its ability to actively swim, enable it to exploit both benthic and pelagic habitats. The ecological versatility may mitigate some ecological disruptions caused by other invasive species and also participate to food-web stability through energetic coupling (Rooney et al. 2006; McMeans et al. 2016). This dual habitat exploitation allows *H. anomala* to adapt to varying environmental conditions and seasonal shifts in resource availability, which likely explains part of its invasive success. For example, its nycthemeral movements into pelagic waters could reduce the negative ecological impact of the energy sink induced by zebra or quagga mussels (*Dreissena polymorpha* and *D. bugensis*) (Yuille et al. 2012; Ives et al. 2013). Some of the nutrients captured by these mussels and released as faeces may be assimilated by *H. anomala* and made available again to consumers such as fish, particularly in areas with high densities of zebra mussels, such as the littoral zones of large lakes (Brown et al. 2022). The ability to reconnect benthic and pelagic food webs particularly relevant in the Laurentian Great Lakes where the process of benthification has been reported (Hecky et al. 2004).

Indirect interactions with native and invaded species

Beyond direct ecological impacts (i.e. predation and competition), *H. anomala* may exert indirect influences on native and invaded communities by altering trophic interactions, habitat use and ecosystem processes. Recurrent *in situ* and direct observations suggest a potential interaction between *H. anomala* and the signal crayfish (*Pacifastacus leniusculus*), with the possibility that the crayfish may provide a kind of refuge against perch predation (Jacquet 2023). While this interaction has yet to be confirmed, this association may facilitate the persistence and local proliferation of *H. anomala* populations in benthic habitats, especially during periods of high predation pressure. In habitats shared with native benthic species, *H. anomala* may indirectly impact these organisms by competing for limited shelter or changing habitat and food availability (Marty et al. 2010; Penk et al. 2018). The presence of *H. anomala* may not only affect species distributions, but may significantly influence broader ecosystem dynamics, including sediment bioturbation and nutrient cycling (Covich et al. 1999; Ricciardi et al. 2012). For example, crustaceans like *Mysis relicta* have been shown to influence oxygen fluxes and sediment biogeochemistry through their bioturbation activity (Lindström and Sandberg-Kilpi 2008). Furthermore, the trophic position of *H. anomala* in aquatic food webs reveals its dual role as a prey item for planktivorous and omnivorous fishes and as a consumer of zooplankton and phytoplankton, potentially disrupting energy flow and nutrient dynamics (Pérez-Fuentetaja and Wuerstle (2014); Fig. 2). By reducing zooplankton grazing pressure, *H. anomala* may indirectly

promote phytoplankton blooms, altering nutrient release and dissolved organic carbon (DOC) cycling (Ricciardi et al. 2012). However, direct consumption of phytoplankton by *H. anomala* can exert a negative effect, reducing biomass at the base of the food web (Ketelaars et al. 1999; Marty et al. 2012; Sinclair et al. 2016). As a result, the net effect on nutrient dynamics fluctuates between positive and negative, depending on specific ecological contexts and trophic interactions. Additionally, this alteration of trophic dynamics could affect higher trophic levels, such as piscivorous fishes, through cascading effects of reduced prey availability (Pérez-Fuentetaja and Wuerstle 2014; Brown et al. 2022). These interactions raise questions about the ecological relationships of *H. anomala* with other organisms and its role in structuring invaded and/or endemic communities.

Management and control efforts

Biological monitoring and early detection

Regular monitoring in aquatic ecosystems is essential to detect *H. anomala* during the early stages of establishment, making it possible to monitor the colonisation front of the species to reduce its spread. Advanced monitoring methods, including environmental DNA sampling (eDNA), have proven efficient and rapid for detecting the species (Cangelosi et al. 2024; Melliti et al. 2025). The possibility of leaving light-based traps in place for control purposes (Brown et al. 2017) adds a new dimension to ecological monitoring.

Control solutions

To prevent and effectively manage the spread of invasive species, it is important to disinfect objects frequently in contact with infested waterbodies, such as fishing gear, boats, trailers, sampling and diving equipment and waders. These items can unintentionally transport live specimens or propagules to new ecosystems. Disinfection is necessary because *H. anomala* can survive on damp surfaces or in residual water, enabling its accidental introduction into non-invaded habitats. Several disinfection methods have been developed and tested to evaluate their effectiveness in reducing the spread of this species. Disinfectant-based aquatic treatments (e.g. Virkon[™] Aquatic, Virasure[™] Aquatic) and the use of steam have demonstrated 100% mortality of *H. anomala* specimens, suggesting here their effectiveness in inhibiting the spread of this invasive species (De Stasio et al. 2019; Coughlan et al. 2020). Treatments show that spraying is less effective than immersion (De Stasio et al. 2019). Additionally, treatment with hot water at 45 °C for 15 minutes resulted in 99% mortality in *H. anomala*, making this protocol a simple, rapid and effective biosecurity method for preventing the spread of this species (Anderson et al. 2015). Finally, drying, although less effective, requires approximately 8 days to achieve significant mortality (Anderson et al. 2015). Exposure to ultraviolet (UV) radiation showed a significant reduction in the survival of *H. anomala*, which has a very low tolerance to UV, reaching a value of 17.8 kJ/m² (Zeisler 2023). These disinfection methods, including UV exposure after validation, should be incorporated into biosecurity protocols to decontaminate equipment and prevent the spread and impact of *H. anomala* within aquatic ecosystems.

Public awareness and invasive species policy

Public awareness of invasive species policy plays a significant role in preventing accidental spread, especially in areas with recreational fishing or boating. Invasive species policies addressing education, such as decontamination protocols for boats and equipment, can reduce the risk of spread. For instance, implementing rigorous cleaning protocols for fishing and water sports equipment and boats is essential to mitigate the risk of unintentional introductions and dispersal (Coughlan et al. 2020; Mohit et al. 2023). This has been proposed for some very aggressive aquatic species during the last decade, for instance for quagga mussels (Wong and Gerstenberger 2015).

Conclusions and future horizons

The ecological role and threats of *Hemimysis anomala*

Hemimysis anomala appears to have invaded virtually all types of freshwater ecosystems, including lakes and rivers worldwide, as well as brackish environments such as the Baltic Sea. While this invasion is no longer in doubt, the consequences, along with the ecological and socio-economic risks, remain poorly understood. This underscores the need for effective monitoring and management strategies. Our study demonstrates the ecological role of this Mysidae within food webs, particularly through its interference with native zooplankton and its ability to exploit a wide range of habitats. This plasticity poses a threat to local fauna as it may promote changes in community structure and dynamics.

Key knowledge gaps and research priorities

Further research is necessary to fill the gaps in existing knowledge about *H. anomala*. These studies should include a detailed analysis of its life cycle parameters in the natural environment, such as reproductive patterns, longevity and population dynamics including swarming events. Notably, gut content analyses reveal that swarming may primarily serve as a feeding function rather than reproduction (Wachala et al. 2025). It is also important to investigate its periods and sites of reproduction, along with its interactions with biotic and abiotic factors, specify the effect of temperature on its reproductive cycle, as well as prey-predator interactions and food resources. More detailed studies of migration and homing behaviour, particularly their energetic demands, physiological drivers such as sensory mechanisms and responses to environmental cues, could also provide valuable insights into the ecophysiology of the animal. As recently observed in *H. margalefi*, which relies on the chemical signature of its habitat to navigate circadian migrations (Derrien et al. 2024), *H. anomala* might similarly depend on such mechanisms. Investigating these processes, particularly by identifying and characterising the chemical compounds involved, would improve our understanding of its behavioural ecology. Although *H. anomala* has established populations in several brackish environments, including the Baltic Sea (Salemaa and Hietalahti 1993; Janas and Wysocki 2005; Kotta and Kotta 2010), almost nothing is known about its long-term persistence and ecological interactions in such habitats. The species' ability to

tolerate variable salinities (Table 1), its reproductive success and its competitive interactions with native and non-native species in estuaries remain insufficiently documented. Additionally, the role of *H. anomala* in nutrient cycling and dissolved organic carbon (DOC) dynamics remains poorly understood. While this species releases nutrients and DOC through excretion and organic matter decomposition, the extent to which these processes influence primary production and microbial activity remains uncertain. Identifying its impact on nutrient remineralisation, microbial interactions and potential contributions to biogeochemical cycles would refine our understanding of its ecological role in aquatic ecosystems. Finally, its influence on higher trophic levels, particularly piscivorous fishes, remains unclear and requires further investigation. *Hemimysis anomala* interacts with these predators both directly, through biomagnification and contaminant transfer and, indirectly, via contrasting trophic effects (Fig. 2). However, its net impact on piscivorous fish populations is not well established. Further research is needed to determine how these mechanisms vary across ecosystems and influence food web stability.

Towards comprehensive monitoring and management

We believe that expanding our knowledge of the distribution of *H. anomala* is another priority. A multi-scale and multi-methods approach combining diving, eDNA and remotely operated vehicle surveys would enable us to map its distribution across and within ecosystems. To refine our understanding of its place in food webs, this will require the application and development of complementary approaches such as underwater video, metabarcoding and immunochemical analyses.

Leveraging citizen science for invasive species monitoring

The creation of participatory diving networks can mobilise recreational divers to report the presence of *H. anomala*, thereby increasing monitoring efforts in often inaccessible areas. These collaborative initiatives not only collect valuable data, but also raise community awareness of the problem of invasive species.

This study demonstrates the potential of citizen science to enhance invasive species monitoring while promoting public engagement in biodiversity conservation. Through participatory diving networks, significant data were gathered on *H. anomala*'s presence, habitat use and seasonality, showcasing the benefits of collaborative initiatives (Appendix 1). Observations were conducted over an annual cycle, recording *H. anomala* occurrences and habitat types. Divers contributed data using standardised questionnaires, which included four habitat categories (e.g. benthic sediments covered by quagga mussels, crevices under rocky outcrops, wrecks and artificial shelters and the water column). They also estimated relative abundances of the species and provided additional information, such as life stages (adult vs. juvenile).

By combining scientific diving with citizen science, this study elucidated a clear seasonal pattern in the habitats occupied by *H. anomala* (Fig. 3). Winter swarms, often exceeding 160,000 individuals in approximately 5 m³ and occasionally occupying volumes up to 100 m³, were widely observed at depths of 10 to 20 metres. In contrast, summer sightings were rare, with individuals sheltering under rocks or at greater depths (approximately 1000 individuals per 5 m³).

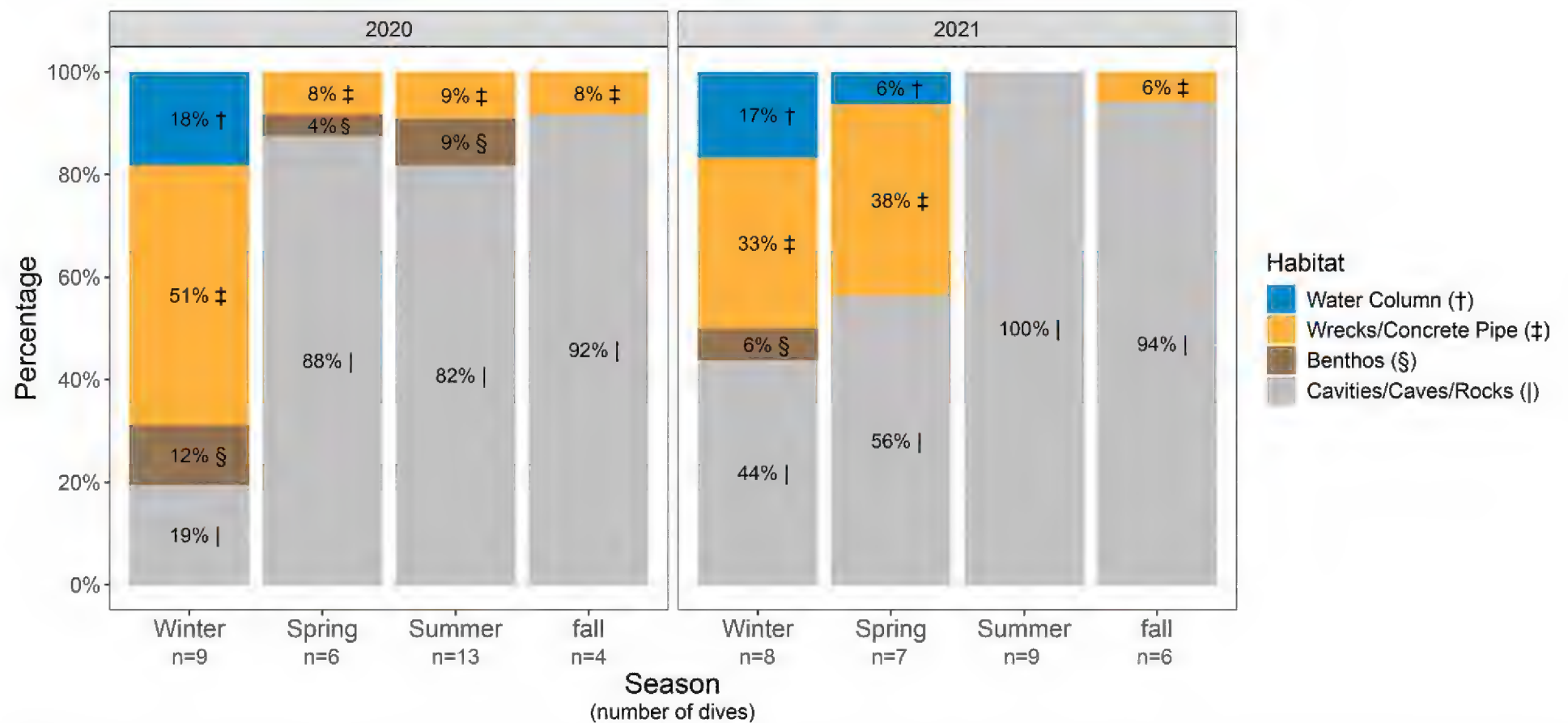


Figure 3. Percentages of habitat types occupied by *H. anomala* observed during the 2020–2021 seasons in Lake Geneva, at the Saint-Disdille pilot site (Thonon-les-Bains, France; Appendix 1). Data were collected through scientific diving and citizen science, with the total number of dives indicated below the bars (n). Observed habitats include the water column (†), anthropogenic structures such as wrecks and concrete pipes (‡), benthic habitats (§) and cavities, caves or rocks (|). The video reveals what winter swarms look like in Lake Geneva (<https://hal.science/hal-04820062>).

This seasonal pattern underscores the ecological flexibility of *H. anomala* and its adaptation to varying environmental pressures. These results demonstrate the value of citizen science in advancing invasive species monitoring, offering both enhanced data collection capabilities and a means of engaging the public in biodiversity conservation efforts.

Conclusion

Despite promising developments, early detection using new methodologies remains under-explored in current monitoring programmes. These tools need to be further integrated to provide an early warning of its presence and better respond to its expansion. These efforts should also include predictive modelling to assess potential geographic and ecological spread, especially under climate change and habitat alteration scenarios. Additionally, participatory research, such as diving, should be conducted to increase public awareness and cooperation, providing valuable data and encouraging citizen engagement in addressing the spread and impacts of invasive species that threaten the biodiversity of aquatic ecosystems.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SJ. Data curation: HR. Investigation: HR, SJ. Project administration: SJ. Supervision: SJ. Visualization: HR. Writing - original draft: JG, HR. Writing - review and editing: HR, VF, JM, SJ.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Appendix 1

Recreational divers as participative citizen science

This appendix provides additional methodological details about the participatory diving study conducted between 2020 and 2021. The primary site was located in Lake Geneva at Saint-Disdille, Thonon-les-Bains, France (46°24'06"N, 6°30'08"E DMS), which is characterized by diverse habitat types.

Observations were made elsewhere, at eight sites in Lake Geneva, two in Lake Bourget (France), and one in Lake Annecy (France) through 120 scuba diving expeditions (63 scientific and 47 recreational; total immersion duration of 72.5 hours) conducted both during the day and at night over an annual cycle to record *H. anomala* occurrence and habitat type.

Data collection relied on questionnaires completed by divers (see Fig. S4). Divers recorded habitat categories (e.g., benthic sediments primarily covered by quagga mussels, crevices under rocky outcrops, wrecks and artificial shelters such as harbors and other submerged structures, and the water column) and estimated the relative abundance of the species (e.g., < 50, 50–100, 100–500, 500–1000, > 5000 individuals) and identified the life stage of the animals (adult vs. juvenile).

The survey revealed important seasonal variations.

- During winter, numerous dense swarms of *H. anomala* were most frequently observed at diving sites. They are widely seen in open water near wrecks and inside them, occupying significant volumes with millions of individuals. The swarms are mostly observed between 10 and 20 meters deep and consist mainly of adult individuals.
- From spring onwards, *H. anomala* swarms are not observed in the water column and become increasingly rare, likely due to high mortality and strong predation pressure exerted by perch, which ascend from the depths during this time of the year (unpublished data). By May, the swarms disappear, and only a few tens to hundreds of individuals, mostly juveniles, are detected under rocks, in holes, on the ceilings of submerged pipes, and/or at greater depths.
- During summer, individuals are difficult to observe and generally shelter at the bottom of crevices, often associated with crayfish, or under rocks and stones. Once, a dense 1-m³ swarm of adults was observed at a depth of 45 m at a diving site in Evian (France), and groups of 10–20 individuals were reported in front of crayfish burrows at depths of 42–54 m (2020).
- During early autumn, the mysids were observed in small numbers under rocks, at the bottom of crevices, but regularly with an increasing number of individuals compared to the summer period. During the second part of autumn, swarms begin to reform and return to open water, devoid of apparent predators. However, it is important to note that during the winter of 2022–2023, a significant absence of swarms was observed, which may be linked to unusually high temperatures that impacted their behaviour and population dynamics (Jacquet, 2023).

Supplementary material 1

Additional information

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Data type: docx

Explanation note: This file includes one table and four supplementary figures.

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